CIRCADIAN AND SEASONAL ACTIVITY PATTERNS OF SYMPATRIC HOG-NOSED (*CONEPATUS LEUCONOTUS*) AND STRIPED (*MEPHITIS MEPHITIS*) SKUNKS

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ABSTRACT

Circadian and seasonal activity of sympatric hog-nosed (*Conepatus leuconotus*, n = 12) and striped skunks (*Mephitis mephitis*, n = 9) were monitored via activity-sensor-equipped radiocollars from 15 October 2010 to 20 November 2011 in west-central Texas. Temperature, average and maximum wind speed, barometric pressure, dew point, moon phase, and time of sunset/sunrise were recorded to evaluate which factors influence skunk activity. Both species exhibited predominantly nocturnal activity patterns with some daytime activity across all seasons. Onset and cessation of activity was highly correlated with sunset and sunrise. Activity during the day was documented in both species for all seasons, and the greatest degree of daytime activity was found in hog-nosed skunks in the spring. Activity patterns were significantly different between species and seasons. Moon-phase, season, time before sunrise/sunset, environmental temperature, barometric pressure, and maximum wind-speed were all shown to significantly impact skunk activity.

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INTRODUCTION

Skunks are one of the most universally recognized groups of mammals and yet most species remain poorly understood. The hog-nosed skunk, *Conepatus leuconotus*, and striped skunk, *Mephitis mephitis*, are two of five species of skunks, family Mephitidae, to occur in North America, all of which are found in Texas.

The hog-nosed skunk is considered the largest North American skunk, characterized by a single, broad white stripe that runs from the top of the head to the base of the tail, and a relatively long, naked, hog-like snout (Schmidly 2004). This species occurs from Nicaragua through Mexico and into the southwestern United States (Dragoo et al. 2003). The hog-nosed skunk is commonly referred to as a "rooter skunk" in Texas due to their foraging strategy, which generally entails use of the characteristic nose for rooting up grubs and other prey items. The diet changes seasonally but consists largely of insects, but includes arachnids, vegetation, reptiles, and occasionally small mammals (Taylor 1953a). Skunks are generally considered nocturnal carnivores but some reports indicate that hog-nosed skunks might exhibit more daytime activity than other skunk species, particularly during midwinter in central Texas (Schmidly 2004).

The striped skunk, *Mephitis mephitis,* is the most common skunk species in Texas (Schmidly 2004). They are medium-sized carnivores, and are characterized by a bifurcate white stripe along the back which joins at the neck; in addition, they always have a distinct stripe on the forehead (Wade-Smith and Verts 1982). Food habits in striped skunks are similar to hog-nosed skunks, with a high degree of insectivorous behavior (Taylor 1953b).

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Unlike the hog-nosed skunk, there have been studies documenting the activity of *Mephitis mephitis* in North America (Aleksiuk and Stewart 1977; Davis 1951; Hamilton 1937; Jones 1939; Lariviere and Messier 1997; Mutch and Aleksiuk 1977; Neiswenter and Dowler 2010 Selko 1938; Smith 1931; Terres 1940; Verts 1963; 1967).

No studies have examined activity of sympatric hog-nosed and striped skunks, though one study addressed activity between striped skunks and *Spilogale gracilis*, the western spotted skunk (Neiswenter and Dowler 2010).

The primary objective of this study was to document typical activity patterns throughout the full circadian cycle throughout the year, and evaluate whether hog-nosed and striped skunks exhibit temporal differences in their times of activity as a method of niche separation. Temporal avoidance is one known strategy for avoidance of interference competition in similar species which occur sympatrically (Carothers and Jaksic 1984), and previously, when sympatric populations of *M. mephitis* and *Spilogale gracilis* were studied, data suggested niche separation occurs in relation to time of activity (Neiswenter and Dowler 2010). Additionally, seasonal pattern fluctuations, extent of daytime activity, and the impact of various environmental variables on activity for sympatric populations of hog-nosed and striped skunks were evaluated.

MATERIALS AND METHODS

This study was conducted from October 2010 to November 2011, on a 3200-hectare site located 15 miles southwest of San Angelo near the community of Knickerbocker (N31.256530° W100.664905°). The annual rainfall in the San Angelo area was 51.13 cm in 2010 and 23.44 cm in 2011, both falling below the average rainfall from 1981-2010 of 53.98 cm. The habitat in this area was characteristic of the western semi-arid Edwards Plateau region with scrub-land, rocky upland, and riparian zones. For this study the appropriate procedures for trapping, anesthetizing, and handling mammals were followed (Sikes et al. 2011). The general protocol was modeled after a recent study on skunk activity (Neiswenter and Dowler 2010) in consideration with other radiotelemetric studies (Garshelis et al. 1982; Lariviere and Messier 1997). Skunks were captured by hand during spotlighting surveys, or in various-sized Tomahawk live traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin). After capture, the skunks were anesthetized using Telazol in a universal dose of 10 mg (Lariviere and Messier 1997), and fitted with a radiocollar weighing 42 grams or less. The radiocollars feature an activity monitor and mortality sensor (Advanced Telemetry Systems, Isanti, Minnesota). The radio-transmitter emitted an erratic rate of pulses when movement was detected, and after movement had ceased, pulse rate immediately defaulted to a 40 pulse/min rate. Skunks were monitored via a handheld telemetry receiver (Communications Specialists Inc.) in conjunction with a vehicle-rooftop-mounted antenna (Laird Technologies).

Ambient temperature, average/ maximum wind speed, barometric pressure, and dew point were documented on an hourly basis using a Nielsen-Kellerman Kestrel 3500 weather meter. Time of sunset, sunrise, and moon phase were also documented for each collection period using data from the U.S. Naval Observatory (www.usno.navy.mil). Moon phase was defined as one of four conditions based on percentage of moon face illumination: new (0-24%), quarter (25-49%), half (50-74%), or full (75-100%).

The study area was visited over different time intervals so as to gather data sampling at all periods of the day throughout the year. During the time intervals, all detectable skunk frequencies were checked to establish a general status of active or inactive per every 15 minutes. In order to confirm activity status, the signals were re-checked twice, each approximately 5 minutes apart (Garshelis et al. 1982). Skunks were determined to be active at a specific time period if at least 2 of the 3 signal fixes in a 15 minute span were active. Inactivity was determined using the same best-of-three approach for each time period. If a particular skunk was out of telemetry range or if the signal was mixed (inactive/active/out of range), the skunk was listed as not available (NA) for that 15 minute interval. The collected data were organized based on time, day, month, season, and moon phase and analyzed via pivot tables in Microsoft Excel search for any obvious trends or patterns. Seasons were defined to mirror those used by Neiswenter and Dowler (2010): spring (breeding season for *M. mephitis* and *C. leuconotus*) from 1 February - 14 May, summer (post-parturition) from 15 May – 31 August, fall (dispersal) from 1 September – 14 November, and winter from 15 November – 31 January.

Statistical analysis was performed with R version 2.12.1(R Development Core Team

2011) in two phases, treating time variables and environmental variables independently. Analysis was structured as a general linear model (GLM) with a logit-link function (Agresti 2002). Each variable was tested for significance using -2log[LRT] (likelihood ratio test) and added to the statistical model one at a time. Once the significant main effect variables were identified, interaction testing was used to determine significant differences in activity between species based on the selected variables. Due to the likelihood of temperature having a quadratic relationship to activity, it was analyzed first as a linear function, then with a quadratic transform function for comparison. The statistical output from R was then used to generate odds ratios which indicate the odds of finding an active skunk based on specific variables and confidence intervals were developed for analyzing the two categorical variables, moon-phase and season.

RESULTS

A total of 12 *C. leuconotus* (8 females, 4 males) and 9 *M. mephitis* (3 females, 6 males) were radio-collared and monitored over the course of the study for a total of 400.5 hours (112.75 fall, 62 winter, 78.5 spring, 147.25 summer) or 1,602 15-minute data-periods with a total of 8,253 data points. Variable values differed substantially between seasons (Table 1). Average number of active skunks at each 15 minute time slot across 24-hr days was plotted by season and revealed a predominantly nocturnal activity pattern (Figs. 1-4). For both species, onset of activity was correlated with time of sunset, and cessation of activity was correlated with time of sunrise. This was most obvious in the spring and summer (Figs. 3 and 4), whereas onset and cessation of *M. mephitis* activity were more gradual in the fall and winter (Figs. 1 and 2). Skunks of both species were found to be active during daylight hours in all seasons, but bouts of daylight activity tended to be brief in duration. The highest degree of daylight activity was exhibited by *C. leuconotus* in the spring. In the fall and winter months, striped skunks tended to be active sooner and cease activity later than hog-nosed skunks. Striped skunks had detected activity well before sunset in the winter. *C. leuconotus* and *M. mephitis* displayed very similar patterns of average activity during the summer months with striped skunks initiating and ceasing activity slightly earlier than hog-nosed skunks (Fig 4).

Analysis revealed 4 time variables and 3 environmental variables as significant in predicting skunk activity for both species. Season, moon phase, hours before sunrise, and hours before sunset were all significant. Moon-phase was eliminated from the model because although collectively significant, individual phase comparison returned mixed results which were deemed unreliable for determining skunk activity (Table 2). Further testing showed that the time-model with both hours before sunset and hours before sunrise was not significantly better than the model with only one of these two variables, so the model was tested twice to identify any differences. Results were the same regardless of which variable was incorporated into the model. The final time-model consisted of species, hours-before-sunrise, and season (Table 3). Temperature, barometric pressure, and maximum wind speed were each significant in the environmental model (Table 4).

The final time model showed significance for all main-effect variables and interactions except for the species by hours-before-sunrise interaction (Table 3). Similarly, the environmental model showed significance for all main-effect variables and interactions except for species by maximum-wind-speed interaction (Table 4). The odds ratios for the intercept and TypeStripe were not included because they were exceedingly large and have no interpretive value. The quadratic transformation of temperature had no appreciable difference on the significance of other variables or interactions within the statistical model. The odds-ratio value (OR = $e^{\wedge(\text{estimate})}$) can be interpreted as the number of times more likely one is to find skunks active for the designated variable, or when the OR value is less than one dividing 1 by the OR value gives the number of times less likely one is to finding an active skunk.

Odds-ratios generated from the seasonal data showed that hog-nosed and striped skunks were both less likely to be active in summer versus fall, 2.9 and 1.4 times less, respectively (Table 5). Hog-nosed skunks were 3.7 times less likely to be active in spring than in fall. Striped skunks were 2.04 times more likely to be active in winter versus fall, while hog-nosed skunks were 1.6 times less likely. Likelihood of activity in spring and summer was less than that for winter in species. Hog-nosed skunks were 2.2 times less likely to be active during spring and 2.6 times less in summer when compared to winter. Striped skunks were 1.7 and 2.8 times less likely to be active in spring and summer versus winter, respectively. The confidence interval for the odds-ratio estimate in spring vs. summer activity for both hog-nosed and striped skunks and the spring vs. fall for striped skunks contained 1.0 and was therefore deemed non-significant.

DISCUSSION

Both species adhered to a predominantly nocturnal activity pattern, as was expected. This was clear despite the fact that sampling effort, consistency/congruence of times sampled, and number of skunks with functional radio-collars varied from month to month. Although no previous study has addressed activity patterns of *Conepatus leuconotus* in North America, there have been other studies documenting species within the same genus, *Conepatus humboldti* in southern Chile (Fuller et al. 1987) and *Conepatus semistriatus* in the Talamanca region of Costa Rica (Gonzalez-Maya et al. 2009), and *Conepatus chinga* in northwestern Patagonia (Donadio et. Al 2001), each of which reported a predominantly nocturnal activity pattern with onset and cessation correlated to sunset and sunrise. *Conepatus semistriatus* was shown to exhibit some limited daylight activity as well (Gonzalez-Maya et al. 2009), not unlike the activity of *Conepatus leuconotus* in this study. Similarly, previous studies documenting *Mephitis mephitis* activity (Aleksiuk and Stewart 1977; Davis 1951; Hamilton 1937; Jones 1939; Lariviere and Messier 1997; Mutch and Aleksiuk 1977; Neiswenter and Dowler 2010 Selko 1938; Smith 1931; Terres 1940; Verts 1963; 1967) show a distinct nocturnal activity pattern closely correlated with sunset and sunrise times as well as decreased activity in the winter in northern North America. Results of this study support the nocturnal patterns found in previous studies, and the additional circadian cycle data showed that short bouts of daylight activity are not uncommon in either species. The data were in contrast to previous studies that have documented diminished activity levels in *M. mephitis* during winter months (Hamilton 1937; Jones 1939; Selko 1938;

Terres 1940; Verts 1967); however, all previous studies were in northern locations. In higher latitudes, striped skunks have long periods of inactivity because of cold weather conditions and snow cover (Terres 1940; Verts 1967; Sunquist 1974). These skunks in Texas remain active throughout the winter season and our data show increased activity over other seasons. The data showing higher likelihood of activity during the winter may have been an artifact of uneven sampling due to limited access to the study site during part of the winter season; however, increased activity could suggest lower prey densities requiring longer foraging times in winter. This pattern could have been exacerbated by the drought conditions that affected the area during the study period. If skunks were unable to maintain high enough energy reserves before the winter, it is reasonable to assume that higher activity might have been necessary to sustain life through the winter. Hog-nosed skunks had the highest likelihood of activity during the fall months which contradicted our initial hypothesis that highest activity would be found in spring and summer when the animals are most likely to be breeding, birthing, and raising young.

Statistical analysis of time variables suggested that season, moon-phase, and hours-before sunrise/sunset are important factors contributing to skunk activity, and the model demonstrated that there are perceivable differences in activity between *C. leuconotus* and *M. mephitis*. The lack of significance for species/season interaction in the winter likely indicates insufficient sampling through that season. This result is not entirely surprising as winter was the least sampled time period over the course of the study. Significant interaction between species and hours before sunrise/sunset in *Conepatus leuconotus* indicated that the activity patterns of hog-nosed skunks are more correlated with sunset and sunrise. This is supported by the graphical representations of activity for each season, where *C. leuconotus* tends to have a sharper cessation of activity around sunrise and a steeper onset of activity around sunset (Figs 1-4). Conversely, *M. mephitis* tends to have less distinct changes in activity which vary across seasons. Even so, activity of both species is correlated with sunset and sunrise times, which is illustrated in the time model by the significance of hours-before-sunrise as a main-effect variable and the lack of significance of the hours-before-sunrise as an interaction with species (Table 3). It is more difficult to interpret the lack of significance between different moon phases. We hypothesized that all moon phases should impact skunk activity in varying degrees and the present results might be due to a lack of adequate sampling or other factors such as cloud cover, temperature extremes, or precipitation. Elimination of moon-phase from the time-model avoided questionable impacts to species, hours-before-sunrise, and season to produce more accurate odds-ratios.

Environmental model analysis revealed that temperature, barometric pressure, and maximum wind speed had significant influence on skunk activity, identifying each as a contributing factor of skunk activity. The lack of significant interaction between maximum wind-speed and species indicates that the variable is useful for predicting skunk activity in both species but not for distinguishing differences between species (Table 4). It is interesting to note that altering the temperature relationship from linear to quadratic had no appreciable effect on the statistical significance of any part of the environmental analysis.

Hog-nosed and striped skunks show statistically significant differences in activity when analyzed using the variables collected in this study. It is obvious that these variables do not provide a perfect activity prediction model, and there are surely some key variables missing, such as precipitation levels, animal health, previous foraging success, percentage of cloud cover, luminosity, and prevalence of potential food items. Although the differences in variables associated with activity between species were significant, we did not observe negatively-correlated peaks in activity which might suggest temporal-based niche separation as a strategy for avoiding interference competition (Carothers and Jaksic 1984). Seasonal patterns varied, and were not as uniform as those previously reported for sympatric *Spilogale gracilis* and *Mephitis mephitis* (Neiswenter and Dowler 2010).

Atypical climatic patterns during the study period likely affected this study. From October 2010 to November 2011, west-central Texas was subjected to some of the most extreme drought conditions ever recorded for the area, which resulted in numerous large-scale wildfires and complete loss of several local water sources. These conditions undoubtedly impacted local skunk populations negatively, and may have resulted in modification of normal activity patterns. Additional analysis methods may also benefit this study. The use of a GLM for this type of binomial experiment can potentially result in erroneous interpretations due to multiple observations being made on the same individual. For each data-point at a specific time, activity in a particular skunk is dependent on whether the skunk was active at the previous point-in-time which creates a potential time dependence error not addressed by a GLM approach. Further research using this GLM combined with generalized estimation equations (GEE) and generalized linear mixed models (GLMM) will help to account for the inherent error in a GLM alone (Zuur et al. 2009).

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Table 1.- Minimum to maximum variable ranges, by season, for data collected during activity study of hog-nosed and striped skunks.

Season	**# of 15min. Data Pts.**	**# of *C. leuconotus* in study**	**# of *M. mephitis* in study**	**Time of sunrise**	**Time of sunset**	**Temperature** (ºC)	**Wind (kph)**	**Barometric Pressure (inHg)**	**Dew Point** (ºC)
Fall	451	1 to 9	3 to 5	7:01 to 8:00	17:45 to 20:07	8.7 to 33.7	0 to 22.5	27.48 to 27.94	-4.5 to 18.3
Winter	248	6 to 9	1 to 5	7:12 to 7:41	17:39 to 18:14	-0.3 to 27.9	0 to 19.2	27.53 to 27.94	-10.1 to 15.4
Spring	314	6 to 9	5 to 8	6:47 to 7:55	18:18 to 20:29	-9.9 to 40	0 to 16.5	27.39 to 27.93	-14.3 to 18
Summer	589	4 to 8	5 to 8	6:37 to 7:14	20:13 to 20:51	15.9 to 42	0 to 21.2	27.36 to 27.9	-6.8 to 20.2

Table 2.- Odds ratios estimates with upper and lower confidence interval values for moon phase.

Species	Comparison	Lower	Odds Ratio	Upper
C. leuconotus	Half vs. Full	0.92	1.32	1.89
M. mephitis	Half vs. Full	1.43	1.93*	2.62
C. leuconotus	New vs. Full	0.48	0.65*	0.88
M. mephitis	New vs. Full	0.74	0.97	1.28
C. leuconotus	Quarter vs. Full	0.37	0.56*	0.83
M. mephitis	Quarter vs. Full	0.57	0.82	1.16
C. leuconotus	Half vs. New	1.45	2.02*	2.81
M. mephitis	Half vs. New	1.53	1.99*	2.6
C. leuconotus	Half vs. Quarter	1.57	2.37*	3.6
M. mephitis	Half vs. Quarter	1.67	2.37*	3.37
C. leuconotus	New vs. Quarter	0.8	1.17	1.72
M. mephitis	New vs. Quarter	0.86	1.19	1.65

Asterisk indicates significance at the 5% level.

Table 3.- Time-model values after moon-phase and hours-before-sunset were removed. "TypeStripe" designates species significance. ":" designates interaction testing between species and hours before sunrise (hbrise) or season.

Coefficients	Estimate	Odds Ratio	Std Error	Z	P
(Intercept)	0.7753	2.17	0.1994	3.89	0.0001*
TypeStripe	-0.6781	0.51	0.2267	-2.99	0.0028*
hbrise	0.0368	1.04	0.0078	4.71	<0.0001*
SeasonSpring	-1.3219	0.27	0.2277	-5.8	<0.0001*
SeasonSummer	-0.9303	0.39	0.2120	-4.39	<0.0001*
SeasonWinter	-0.4973	0.61	0.2406	-2.7	0.0388*
TypeStripe:hbrise	0.0016	1.00	0.0105	0.15	0.881
TypeStripe:SeasonSpring	1.0843	2.96	0.2754	3.94	<0.0001*
TypeStripe:SeasonSummer	0.7653	2.15	0.2468	3.1	0.0019*
TypeStripe:SeasonWinter	0.937	2.55	0.3275	2.86	0.0042*

Asterisk indicates significance at the 5% level.

Table 4.- Environmental-model values after quadratic transformation of temperature. "TypeStripe" designates species significance. ":" designates interaction between species and max wind speed (MWS), barometric pressure (Press), or quadratic-transformed temperature ($Temp^2$).

Coefficients	Estimate	Odds Ratio	Std Error	Z	P
(Intercept)	51.4839	a	13.2699	3.88	0.0001*
TypeStripe	40.6334	a	17.8896	2.27	0.0231*
MWS	-0.0390	0.96	0.0132	-2.96	0.0031*
Press	-1.8306	0.16	0.4783	-3.83	0.0001*
$Temp^2$	-0.0013	0.99	0.0002	-8.46	< 0.0001*
TypeStripe:MWS	0.0293	1.03	0.018	1.63	0.1031
TypeStripe:Press	-1.4511	0.23	0.6446	-2.25	0.0244*
TypeStripe:$Temp^2$	-0.0007	0.99	0.0002	-3.24	0.0012*

[a]Odds ratios for Intercept and TypeStripe were not included because they were exceedingly large and had no interpretive value. Asterisk indicates significance at the 5% level.

Table 5.- Odds-ratios for seasonal activity with upper and lower confidence intervals.

Species	Comparison	Lower	Odds Ratio	Upper
C. leuconotus	Spring vs. Fall	0.17	0.27*	0.43
M. mephitis	Spring vs. Fall	0.56	0.77	1.05
C. leuconotus	Summer vs. Fall	0.22	0.35*	0.53
M. mephitis	Summer vs. Fall	0.55	0.72*	0.93
C. leuconotus	Winter vs. Fall	0.37	0.61*	0.98
M. mephitis	Winter vs. Fall	1.29	2.04*	3.23
C. leuconotus	Spring vs. Summer	0.59	0.80	1.06
M. mephitis	Spring vs. Summer	0.81	1.07	1.41
C. leuconotus	Spring vs. Winter	0.30	0.45*	0.67
M. mephitis	Spring vs. Winter	0.23	0.38*	0.60
C. leuconotus	Summer vs. Winter	0.40	0.57*	0.80
M. mephitis	Summer vs. Winter	0.23	0.35*	0.55

Asterisk indicates significance at the 5% level.

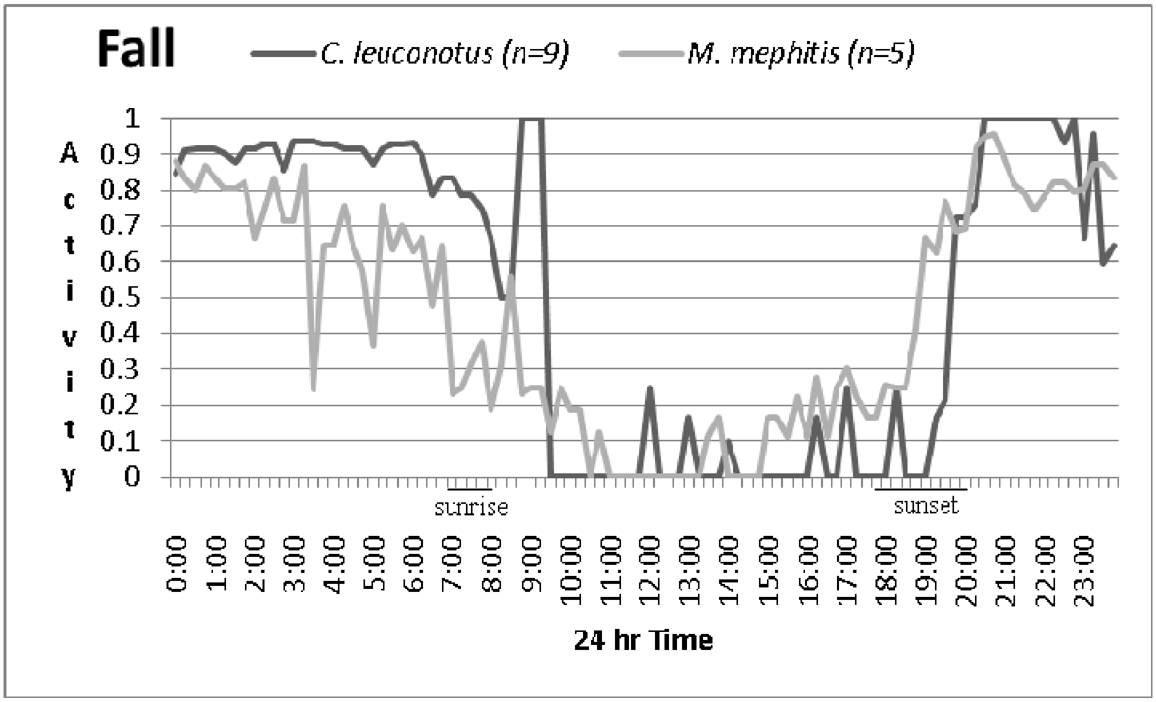

Fig. 1- Circadian activity patterns for sympatric hog-nosed (*C. leuconotus*) and striped skunks (*M. mephitis*) for summer. Fractional percentage of skunks active (Y) plotted over the full circadian (24 hour) cycle (X) from 1 September to 14 November. Sunrise and sunset time range for the season is indicated by designated lines.

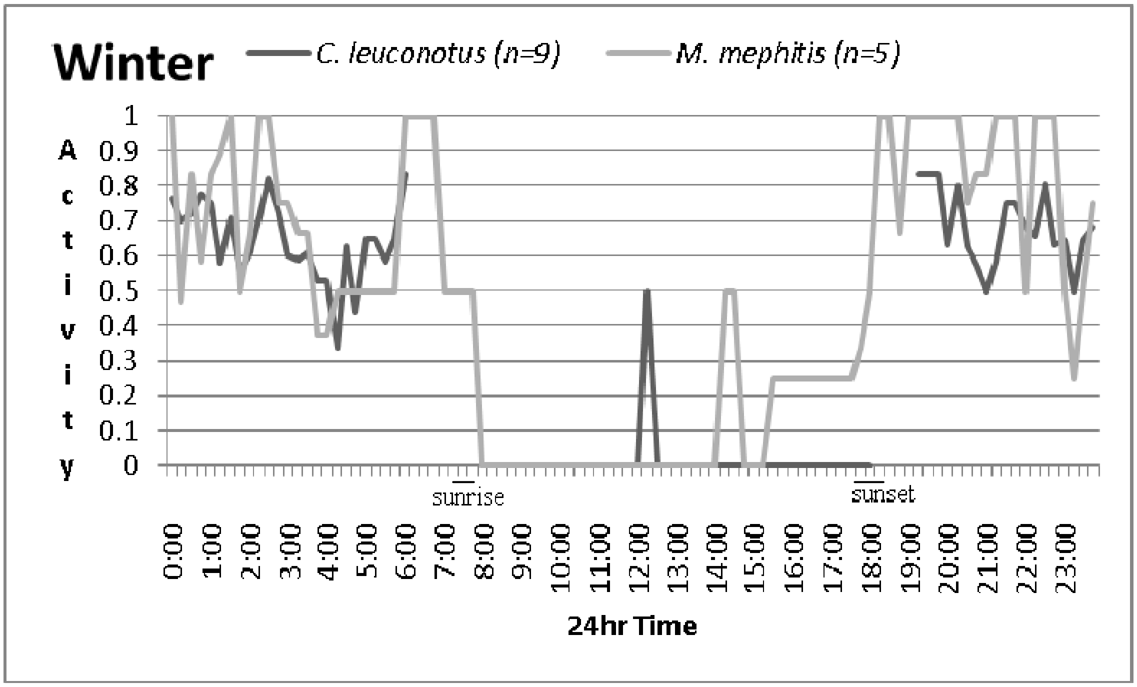

Fig. 2- Circadian activity patterns for sympatric hog-nosed (*C. leuconotus*) and striped skunks (*M. mephitis*) for winter. Fractional percentage of skunk activity (Y) plotted over the full 24 hour circadian cycle (X) from 15 November to 31 January. Sunrise and sunset time range for the season is indicated by the designated lines. Gaps in the graph indicate lack of sampling for that specific period of time.

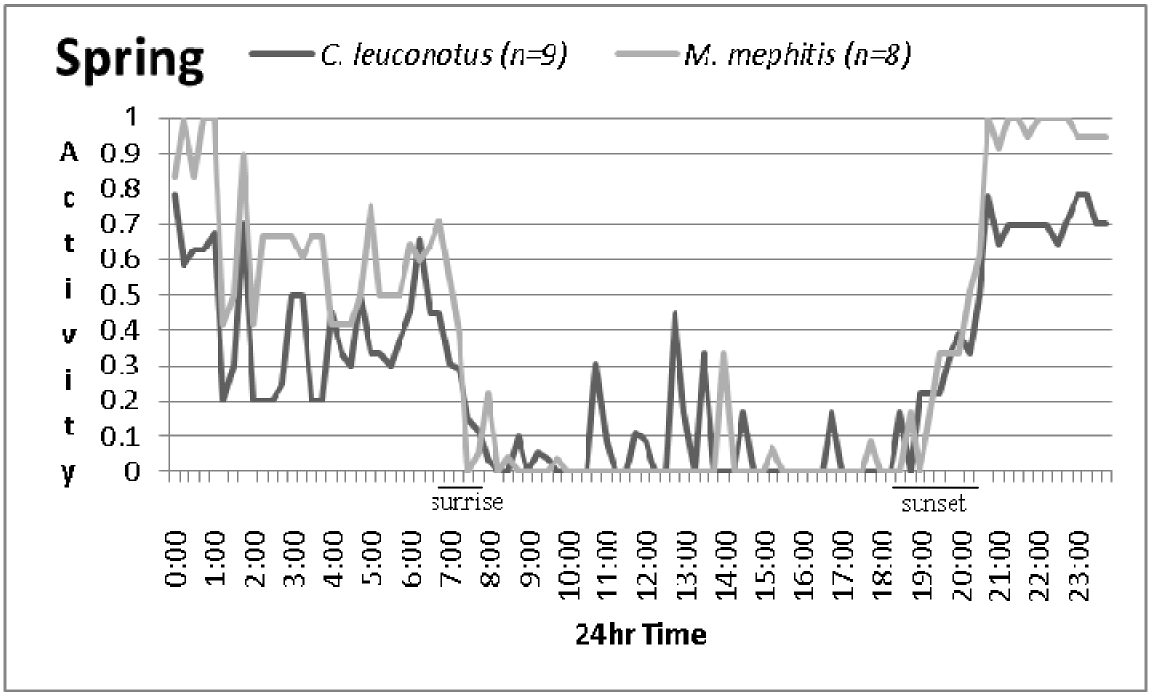

Fig. 3- Circadian activity patterns for sympatric hog-nosed (*C. leuconotus*) and striped skunks (*M. mephitis*) for spring. Fractional percentage of skunk activity (Y) plotted over the full 24 hour circadian cycle (X) from 1 February to 14 May. This period coincides with breeding season in both species. Sunrise and sunset time range for the season is indicated by the designated lines.

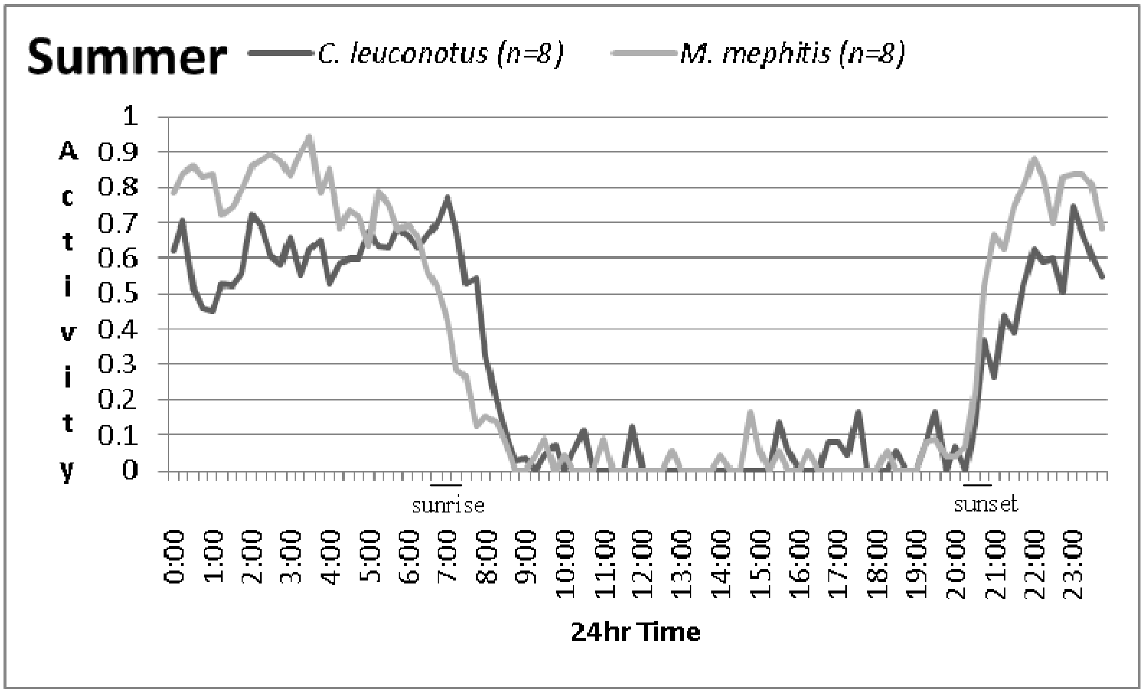

Fig. 4- Circadian activity patterns for sympatric hog-nosed (*C. leuconotus*) and striped skunks (*M. mephitis*) for summer. Fractional percentage of skunk activity (Y) plotted over the full 24 hour circadian cycle (X) from 15 May to 31 August. This period coincides with post-parturition and rearing of young. Sunrise and sunset time range for the season is indicated by the designated lines.